CONTRIBUTION TO A KNOWLEDGE OF AUSTRALIAN *HIRUDINEA*. PART V. LEECH-METAMERISM.

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(Plate iii.)

The subject of "Metamerism in the Hirudinea" has for a long time attracted the attention of workers on the group. It has long been known that the annuli which appear on the surface of the leech do not represent true segments or metameres, but that in each genus more or less typically a certain number represent conjointly the limits of a somite. The number of annuli thus entering into the constitution of a somite is, as a rule, constant fundamentally in each genus, although in connection with the extension of the somite variations may take place in the various species of a genus. This, however, happens in but few genera in comparison with the number in which the number of annuli entering into the formation of the "unabbreviated" somites is constant, and characteristic of the genus. At either extremity of the body are found "abbreviated" somites, that is, segments which do not comprise the full number of annuli as found entering into the formation of the complete somite which is present in the middle region of the body. These "abbreviated" somites, when their exact limits have been carefully mapped out, throw much light on the mode of formation and order of origin of the annuli, as we pass from the hypothetical primitive and uniannulate condition of the somite. For our present day conception of the limit of the somite we are indebted mainly to Castle and Moore.

From a study of the nervous system it is evident that 34 somites are represented potentially in the body of all members of the *Hirudinea*, the number of these visible on external examination of the leech being always much less. In the ventral nerve-chain lie 21 distinct, normal, ganglionic masses, and in addition at either extremity lies a much swollen ganglionic mass. These latter terminal aggregations of the ventral chain represent the fused ganglia of 13 somites, of which those represented in the anterior terminal mass are represented externally as "abbreviated" somites at the anterior extremity of the body. The somites denoted by the capsules of the posterior terminal ganglionic mass are not represented externally on the body as segments. From this we can conclude that the missing somites of the posterior extremity are represented in all the various groups of the *Hirudinea* by the posterior sucker; and, furthermore, that in the *Ichthyobdellidæ* a number of the anterior somites are represented in the "capula." In support of this it may be stated that the posterior sucker often shows a faint annulation, and the same is often to be noted in connection with the capula of the *Ichthyobdellidæ*. Again, it is only by this means that we can make the position of the genital apertures in the *Ichthyobdellidæ* coincide within somite-limits with that found in the *Glossiphoniidæ*, *Gnathobdellidæ*, and *Herpobdellidæ*, inasmuch as the genital apertures in the *Ichthyobdellidæ* are more anteriorly situated, if one reckons from the first visible annulus behind the capula.

If we are to regard the *Hirudinea* as having been descended from an Oligochaetan stock, we must regard the ancestral form as a uniannulate worm whose body consisted of 34 distinct somites. More will be said in reference to this after the description of the somitic constitution of a number of forms which I have had the opportunity of examining.

In a study of various genera in which the number of annuli entering into the constitution of a typical somite is different, one has some opportunity of deciding definitely the order of origin of the annuli, and the significance of the same as bearing on the generic importance of that annulation. In my studies in this connection I have assumed the uniannulate condition as being the primitive one, and in this subject for consideration the question is raised as to which annulus of the somite represents potentially that hypothetical primitive ring.

In many leeches there occur, on special annuli, certain sensory papillæ which are more important and prominent than any others which may be developed on the remaining annuli, and these papillæ serve as an indication of the somite-arrangement and constitution. Among other externals which are of the same assistance may be mentioned the nephridiopores, whose position relative to that of the main sensory papillæ is constant. It was only natural that these two structures should have been taken by earlier workers as external signs of the metamerism, as it was readily corroborated by a study of the central nervous system; and it can be readily understood that Whitman should have assumed that the annulus bearing the sensory papillæ represented the first ring of a somite (this annulus carrying also the nerve ganglia), and that the nephridial aperture lay in the last annulus of the somite. Whitman's idea in this connection was upheld until Castle, in 1900, came to the conclusion, from a detailed study of the nervous system, that the limits of a somite were to be recognised from a knowledge of the neuromerism, and from a study of this he came to the conclusion that the sensory annulus represented in general not the first but the middle or potentially middle annulus of the somite. He has further worked out the order of abbreviation, etc., at either end of the body, pointing out that the sensory ring was the most stable of the component annuli of the somite, and that the other annuli were in the first place derived from this sensory annulus by divisions of it anteriorly and posteriorly.

Castle's conclusions have, in the main, been supported very strongly by Livanow's excellent detailed work on the nervous system.

In view of the results obtained by these workers, the opinion of present day students must be that the sensory annulus denotes the middle or potentially middle annulus of the somite.

I have had occasion, in mapping out the somitic constitution of various Australasian representatives of the group, to test Whitman's and Castle's methods of determining somite-limits, and the conclusions are interesting in that they show that considerable variation takes place in various genera regarding the manner of origin of the annuli; and that, while Castle's conclusions are found to be correct in the greater number, in other forms there is a great divergence from the conditions which obtain in the former. From a study of these, the importance of the somitic constitution as a generic character has been found to depend on the manner of the origin of the annuli.

Limnobdella australis.—This leech, for all practical purposes as far as this discussion is concerned, may be considered as belonging to the genus *Hirudo*, inasmuch as it has the same number of annuli, same pentannulate somite, position for the eyes and genital apertures, same number and position of nephridiopores, and the general anatomy is very closely related. Consequently, we can safely conclude that it has the same somitic constitution throughout as in those forms which would fall within the limits of the genus *Hirudo* in its more narrowed sense. In this way we can derive assistance in the study of the metamerism of *Limnobdella australis*, inasmuch as we find metameric sense-papillæ very well developed in such forms as *Hirudo medicinalis*, and one can most legitimately use the position of these structures as if they were present in *L. australis* itself. What is now to be stated in connection with the metamerism of *L. australis* applies equally well to all species of the *Hirudinea* which would fall within the limits of the diagnostic characters of *Hirudo* in its wider sense; that is, all species which possess 102 annuli, and have the eyes situated on annuli 1, 2, 3, 5, and 8, and the genital apertures situated in annuli 30, 35, and 36 respectively.

According to Whitman's scheme and Castle's scheme respectively, we find the metamerism of the anterior extremity to be as follows :—

Somite.	Annuli (Whitman).	Annuli (Castle).
i.	1	1
ii.	2	2
iii.	3, 4	3, 4
iv.	5, 6, 7	5, 6
v.	8, 9, 10	7, 8, 9
vi.	11, 12, 13	10, 11, 12
vii.	14, 15, 16, 17, 18	13, 14, 15, 16
viii.	19, 20, 21, 22, 23	17, 18, 19, 20, 21

It is now regarded by most workers on the group that the somite consisting of a few annuli is more primitive than that which is multiannulate, and with this view I am in accord. This view is then, in effect, that annulation of the segment is a secondary character. Consequently when we find two annuli intimately fused we must regard this state of affairs as the result of an incomplete differentiation and not of abbreviation.

Now we find in *L. australis* that annuli 5, 6, and 7, 8 are well differentiated from each other respectively on the dorsal side, but they are fused ventrally. This shows clearly that 5 and 6 belong to one and the same somite, 7 and 8 to another somite. This being so, it must then be concluded that the sense-papillæ represented by the eyes situated on annulus 8 do not lie on the first annulus of the somite. If Whitman's scheme applied in this case, then we should have the absurdity of an annulus in one somite originating from that in another somite. In the table given above, I consider the annuli as distributed according to Castle's scheme to be the correct one. On the assumption that, at the extremities, we find the somite developing through the same stages through which the pentannulate somite passed, and that no "fusion" has taken place at all, we find that somite iv. consists of two annuli of which the first is sensory; the second annulus has arisen posterior to this annulus, but, inasmuch as it is still fused with it ventrally, the differentiation is not yet complete. In somite v., we find there are three annuli, the middle one of which is the sensory annulus; the posterior ring of the somite is quite distinct dorsally and ventrally from the sensory ring, but the anterior annulus is still fused ventrally with, or rather not yet differentiated from, the sensory ring. Passing now to somite vi., we find the segment consisting still of three annuli, all distinct from each other. In somite vii., there are four annuli, the sensory ring being placed second; and in somite viii., we find the first complete number of annuli.

From these facts it will be seen that we have a complete series showing the development from the uniannulate somite of the extremity of the body to that which is pentannulate; and in *L. australis* we get clearly the order of development of the annuli in the somite, a fact which is most important in connection with the condition of the complete somite. It will be seen, from the facts stated above, that the sensory annulus gives rise by division to another annulus posteriorly, later another anteriorly; then a fourth develops at the posterior extremity of the somite, and finally a fifth annulus at the anterior extremity. This is exactly in keeping with the ideas of Whitman, Bristol, and Castle in this direction.

Orobdella.—This Japanese genus is represented by three species of which *O. Whitmani* is tetrannulate, *O. Ijimai* has six, and *O. octonaria* has eight annuli entering into the formation of the "unabbreviated" somite. We may reasonably regard *O. Whitmani* as exhibiting the most primitive condition as regards the constitution of the somite for the genus. As it has been shown, in the case of *Philæmon*, *Pontobdella*, and *Ozobranchus*, that the sensory annulus represents the third ring of the adult tetrannulate somite, we may, with every reason, conclude that the same holds in *O. Whitmani.* This means that in this species the ganglion of the ventral chain in the middle region of the body is found in the third annulus of the somite, and the nephridiopores on the posterior margin of the second annulus.

Considering now the three species of *Orobdella* from this standpoint, and examining the genital region, we find that the male genital pore in the species is situated in reference to the sensory annulus as follows :—

O. Whitmani in 2nd annulus anterior to ganglion.
O. Ijimai in 3rd ,, ,, ,,
O. octonaria in 4th ,, ,, ,,

The nephridiopores are situated in *O. Whitmani* and *O. Ijimai* on the posterior margin of the annulus preceding that in which the ganglion lies. In the case of *O. octonaria* the ganglia lie in two annuli, and the nephridiopores on the posterior margin of the annulus preceding the more anterior of these two annuli, so that we may conclude that the same two annuli represent the sensory annulus of *O. Whitmani* and *O. Ijimai*, and further that the nephridiopores occupy the same relative position as in the latter two species. Again, from the fact that the ganglion is so situated in *O. octonaria*, we may conclude from comparison with the other two species that the sensory annulus remained quite stable as regards somite-extension or increased annulation in the passage of the somite from the tetrannulate condition of *O. Whitmani* to that exemplified in *O. Ijimai* with its somite composed of six annuli. Later, however, in the passage to the condition of the somite composed of eight annuli this sensory annulus underwent division as shown in the manner above described in *O. octonaria*. In the diagram shown in illustration of this I have attempted to map out the order of origin of the annuli. Somite-extension more readily affects the extreme annuli of the somite, and we find that the anterior and posterior annuli of the tetrannulate somite have divided to give rise to the somite of six annuli. One may prove this by stating that, in the *Hirudinea* in general, the terminal annuli are more prone to divide; that, further, the sensory annulus, for reasons given above, appears not to have been concerned in this stage; that the genital aperture lies in the third annulus in front of the ganglion in *O. Ijimai* instead of being found in the second annulus reckoned in the same way in *O. Whitmani*, thus proving that another annulus has been added in front of the sensory annulus, and this could have taken place only by division of annulus 1, and not of annulus 2; that another annulus has been added at the posterior region, and only annulus 4 could have been concerned in this. In considering the passage now from the somite of six annuli to that of eight annuli we find, as shown above, that the sensory annulus has divided, and that no further annulus has been added posteriorly. The only point to consider now is whether 1a, 1b, or 2 has divided to give rise to the extra annulus anterior to the ganglion. As the sensory ring is usually so stable, but has been proved to divide in this case, it would seem very probable that a division has taken place in 2 also. The order of appearance of these annuli would then appear to be as shown in the diagrams illustrating the constitution of these species. (Plate iii., figs. 1A, 1B, 1C.)

Pontobdella macrothela Schmarda.—The specimen of this species which I had the opportunity of examining, offered special interest for the study of the somite in that genus, inasmuch as the limits of the somite are very clearly shown on external examination without entailing any reference to papillæ, etc. In this species the somite is triannulate, and the annuli constituting the somite consist of one very wide, and two equally small. The annuli are found to be arranged so that the large ring is very intimately bound up with a small one anterior to it, and another posteriorly situated. The line of division between any two small annuli is denoted by a very strongly marked groove so clearly that, on a very casual glance, one could easily determine the limits of a somite without reference to papillæ. The annuli are all provided with prominences, but, in the case of the large annuli, the arrangement and importance of development are quite different. It is this large annulus which corresponds to the large papilliferous annuli of other species of *Pontobdella*, such as *P. australiensis* and *P. muricata*. The only abbreviated somites to be noted occur towards the posterior extremity, and here it is found that a biannulate somite is represented by a large anterior annulus (sensory), and a small posterior annulus. This constitution for a biannulate somite is by far the commoner in all members of the *Hirudinea*.

In some cases the somite of *Pontobdella* consists of four annuli, and then, says Castle, "Apparently, however, it is at the anterior end, for in these animals which I have had an opportunity to examine, the new ring appears to be united more closely with the ring which precedes than with that which follows a sensory ring. Moreover the ring which precedes the sensory ring is usually not so broad as the one which follows it. This is an indication that it is the former rather than the latter which has undergone division." I have not yet had the opportunity of examining a species of *Pontobdella* in which the somite consists of four annuli, but Castle's observations show very clearly that in such forms the third annulus is the sensory ring.

Ozobranchus branchiatus.—Lately I have had the opportunity of examining specimens of this form, and, inasmuch as the species has not been noticed and examined in detail since Menzies described it in 1791, the metamerism of such a species, since the nature of the leech-body morphologically has been variously interpreted since that time, should offer some little interest.

In the "neck"-region of the young individual eight distinct somites can be made out, and, judging from the intimacy of the connection of the annuli, the limits of a somite are clearly marked off. Each somite consists of an anterior annulus which is twice the size of a posterior small annulus. In most instances, also, but particularly in the posterior region of the "neck," there is a more than faint indication of division in the large anterior annulus, so that the somite is foreshadowed in its triannulate condition. This fact shows that the large anterior annulus represents within itself potentially the original primitive annulus of the uniannulate somite; further, that the posterior annulus of the somite is formed and definitely differentiated before traces of the anterior annulus can be made out; and, again, the middle annulus of the triannulate somite represents the primitive ring. This is in keeping with what is to be observed in most cases in regard to the order of development of annuli towards the constitution of a triannulate somite, namely, that the annuli are developed alternately posteriorly and anteriorly to the sensory annulus. The anterior extremity, or "head," although not forming a distinct "capula" as in other Ichthyobdellids, represents a number of fused annuli or somites whose lines of division are not shown externally on the body-surface, beyond that the margin of the "head" is furrowed as far as the midline.

Semilageneta Hilli.—In my original description of this genus I pointed out that the somite was triannulate, and that the limits of the somites were denoted in the anterior part of the body by the presence of distinct papillæ, and in the remaining body-portion by the outline of the body which was divided into segmental regions, consisting of three annuli, by well marked sulci. These areas I still consider to represent distinct somitic divisions. Passing forwards from xii., which is the first of the somites thus marked off, we find xi. triannulate and carrying papillæ on the first and not on the second or middle annulus. This distribution of the papillæ then agrees with Whitman's plan and not with that of Castle.

Addendum to original description.—I originally placed *Semilageneta* among the *Glossiphoniidæ*, but, judging from the position of the genital aperture, it should find its place among the *Ichthyobdellidæ*. The nature of the anterior extremity, however, is distinctly intermediate between that found in the *Ichthyobdellidæ* and *Glossiphoniidæ*, there being no capula developed as in the former of these two groups.

Philæmon pungens.—In examining some killed specimens of this species, my attention was attracted to a regular separation of groups of annuli on the ventral surface, and, strangely enough, these groups consisted of four annuli. The leech is readily seen to be tetrannulate from the distribution of the papillæ. The furrows or gaps which occurred on the ventral surface, dividing off groups of four annuli, seem, then, to mark off the somite-limits, inasmuch as the number of annuli composing the groups was the same as that entering into the somitic constitution, and their presence seemed to donote a more intimate connection of the annuli composing each group, with each other than with the annuli of another group.

On this reasonable assumption it was found that the sensory annulus was denoted by the third annulus of the somite. It has been definitely proved that the sensory annulus occupies the same position among two of the other three tetrannulate forms—*Pontobdella* and *Ozobranchus branchiatus*—so that we can safely conclude that the somite-limits are thus definitely shown by the assistance given by the furrows mentioned above, and that the sensory annulus is the third ring of the adult somite.

Reasons will be advanced later to show that all the tetrannulate leeches are similarly constituted in this respect.

Geobdella tristriata.—In examining a single specimen of this newly proposed species, gaps somewhat similar to those observed in the case of *Philæmon pungens* were noted, and these are evidently due to a buckling of the body as the resultant of the effect of the killing fluid. These I proved, in the case of *Philæmon*, to mark off the somite-limits, so that I have reasonably concluded that the same holds in this case. *Geobdella* is a pentannulate genus. In the two Australian species there are well developed papillæ, but I was unable to detect any such structures in the killed specimen of *G. tristriata.* However, inasmuch as the eyes have the same disposition, and the number of annuli is the same in all species, I have legitimately made use of the disposition of the papillæ as denoted in the other species, in mapping out the position of the sensory annulus in *G. tristriata.* In the manner denoted above, the greater part of the body is divided up into groups consisting of five annuli; and, by taking into account the position of the papillæ in the other species and the position of any of the above-mentioned gaps, I found that the sensory annulus was denoted by the first annulus of the pentannulate somite.

It is interesting to note that in *Philæmon* and *Geobdella*, which anatomically are closely allied, the somite-limits were denoted in the peculiar manner indicated above. The fact that this occurs in both, would seem to lend additional weight to the argument that the gaps do signify the dividing lines of the somites.

It is interesting to note that two of our Australian genera, *Semilageneta* and *Geobdella*, which are thus unique among the *Hirudinea*, as far as we know at present, in that the somite-extension has affected only the posterior region of the somite, thus leaving the sensory ring at the anterior extremity of the somite, have also other unique characters which are of some note. As mentioned previously, *Semilageneta* resembles in many respects the *Glossiphoniidæ*, and again the *Ichthyobdellidæ*. It is a Rhynchobdellid leech, but does not find its place definitely in either of the two divisions of that group. Again, *Geobdella* is unique in that it possesses only two jaws and has the genital apertures separated by seven and a half rings although the somite is pentannulate. This latter peculiar character of *Geobdella* may be due in some measure to the unique manner in which the annuli have been generated in connection with somite-extension.

Another noteworthy feature about *Semilageneta* is that there has been an absorption of somites at the anterior extremity, analogous to the fusion of the anterior somites to form the capula of the *Ichthyobdellidæ*; and further, inasmuch as this absorption, judging from the position of the genital apertures, could only have affected a few somites, there must have been a great absorption of somites at the posterior extremity, since the number of somites represented externally is so very small in comparison with other leeches.

Semilageneta like *Ozobranchus* may yet have to be regarded as a type of a new family intermediate between the *Ichthyobdellidæ* and the *Glossiphoniidæ*.

Conclusions.—We must regard the *Hirudinea* as having been descended from an Oligochaetan-like worm which was uniannulate, and whose body consisted of 34 distinct somites. This represented the condition of the primitive ancestor of the group, as it left the main stem of the phylogenetic tree of the Annulata. Special structures, such as the anterior and posterior suckers were developed, and in the generation of these were concerned the segments at the anterior and posterior extremities. In this connection took place the fusion of the ganglia of the originally distinct segments at these extremities. The traces of annulation sometimes visible on the posterior suckers of members of the *Hirudinea* in general, and sometimes on the capula of the *Ichthyobdellidæ*, support this view. Later came the necessity for the extension of the somite in order to enable of an extension of the body, and this represents the direct reason behind the annulation of the leech-body, inasmuch as, apparently, the somite was incapable of giving rise to another distinct somite, or in other words there has been no increase in the number of ganglia, although the nervous system has given rise to special branches for the innervation of the newly acquired annuli which are so supplied quite separately from the original primitive sensory annulus, which represented, in fact, a sensory unit. This extension of the somite has been concerned chiefly in connection with the greater part of the body which may be termed more or less "central." We find the intermediate stages in the passage from the uniannulate to the multiannulate stage represented in proper serial order, passing from either extremity to that portion of the body in which the complete annulation characteristic of the genus is found. In these intermediate somites we find the key to the order of development of the annuli, and this order, although very different in each of many genera, is constant in the species of any one genus. It may not be out of place to remark here, that we find in such forms as *Branchiobdella* and *Bdellodrilus* a representative very closely allied to the hypothetical primitive ancestor of the *Hirudinea* at the time of its leaving the main stem, or very soon after. These organisms, although certainly not members of the *Hirudinea*, may represent in themselves, and probably do, examples of homoplasy, in that they have developed suckers; still they serve at the same time as examples of what has been said above.

Passing on from the uniannulate condition, we meet with *Microbdella* which is biannulate in the adult state of the somite. In this case the second annulus has been added posterior to the sensory annulus. By the addition of another annulus anterior to these, we meet with the normally developed triannulate adult somite which is so prevalent among the members of the *Rhynchobdellidæ.*

Mesobdella, a distinctly Arhynchobdellid leech, represents the only member of that group, in which the somite retains its simple triannulate nature.

In some cases, however, we find that the third annulus developed is posterior to the second; in other words, that the sensory annulus represents the first annulus of the somite; examples of this are found in only a few genera such as *Semilageneta* and *Geobdella.* Such might well be expected as a variation even in the development of the "fundamental" triannulate somite, inasmuch as we find considerable variation in the order of development of the extra annuli in the evolution of the multiannulate somite. As far as I know, there is not one known instance among the *Hirudinea* in which the second annulus of a somite is developed anterior to the sensory annulus. After this annulus has been developed, it would seem then that two lines allowing for variation are opened up. In the majority of cases we find the third annulus developed anteriorly, but in some posterior to the second annulus. In the latter case, such as in *Semilageneta* and *Geobdella*, we find the sensory annulus represented by the first ring of the triannulate somite. The stimulus given to the exclusive division of the posterior annulus of the somite results in the formation, in *Geobdella*, of a pentannulate somite, the most anterior annulus of which is the sensory ring, and is to be regarded as representing potentially the primitive annulus of the somite.

In the following table is given a list, as complete as possible, of the more important of the known genera of the *Hirudinea*, and idicating the annulation of the various genera of the *Ichthyobdellidæ*, *Glossiphoniidæ*, *Herpobdellidæ*, and *Gnathobdellidæ.*

Order RHYNCHOBDELLIDÆ.

Suborder ICHTHYOBDELLIDÆ.

Genus.	Annuli in Somite.
Branchellion	3
Ozobranchus	3 rarely 4
Pontobdella	3 or 4
Cystobranchus	7
Trachylobdella	3, 6
Callobdella	6
Piscicola	12, 14
Semilageneta	3

Suborder GLOSSIPHONIIDÆ.

Genus.	Annuli in Somite.
Glossiphonia	3
Helobdella	3
Hæmenteria	3 dorsal. 5 ventral.
Placobdella	3
Hemiclepsis	3
Microbdella	2

Order ARHYNCHOBDELLIDÆ.

Suborder HERPOBDELLIDÆ.

Genus.	Annuli in Somite.
Herpobdella	5
Dina	5
Trocheta	6, 7, 8, 11
Dineta	5
Orobdella	4, 6, 8

Suborder GNATHOBDELLIDÆ.

Genus.	Annuli in Somite.
Hirudo	5
Limnobdella	5
Hirudobdella	5
Macrobdella	5
Philæmon	4
Geobdella	5
Hæmadipsa	5
Mesobdella	3
Xerobdella	5
Cylicobdella	
Lumbricobdella	
Limnatis	5
Haemopis	5

In only four genera of the *Hirudinea* is the complete somite known to consist of four annuli. In this category fall species of *Pontobdella*, *Ozobranchus Margoi*, *Orobdella Whitmani*, and *Philæmon pungens*. In all these forms it appears that the sensory annulus is represented by the third ring. This fact is of some special interest in the study of the order of development of the annuli from the uniannulate to the multiannulate condition of the somite, especially as it bears directly on the question of generic differences as regards the nature of the somite of the various leeches. It would seem that the order of the appearance of the annuli in these tetrannulate genera is different from that in such a pentannulate form as *Hirudo*, and furthermore that this is very possibly the reason that these forms are tetrannulate, etc., and not pentannulate. For example, in somite vii., of *Limnobdella australis*, or in fact of any species which falls within the limits of the characters given for the old genus *Hirudo*, we find four annuli. It is the second and not the third annulus in the latter which represents the sensory ring. I have already shown that somite iv. is biannulate, and somites v. and vi. triannulate in *L. australis*, and that in the former somite the anterior ring is sensory and both its component annuli partly fused. Again in somite v., the middle annulus is sensory and the anterior ring is partly fused with this, but the posterior annulus is distinctly differentiated. This shows clearly that the posterior annulus is the first non-sensory annulus to appear, and that the order of appearance of the various annuli of the somite is as follows :—

Annuli	1	2	3	4	5
Order of development ...	e	c	a	b	d

As has been clearly shown in the case of species of *Pontobdella*, and *Ozobranchus branchiatus*, the fourth annulus of the somite is represented by the anterior annulus of the tetrannulate somite. The order of appearance of the various annuli would then be as follows :

Annuli	1	2	3	4
Order of development	d	c	a	b

Inasmuch as this holds in the case of all the *Hirudinea* in which the adult somite is tetrannulate, and the former order in the case of most pentannulate forms, it seems reasonable to conclude that the effect of this variation is reflected in the nature of the adult somite. In connection with this question I might mention that in *Hæmenteria* we find the somites triannulate dorsally but pentannulate ventrally. This condition evidently obtains in all specimens which may be deemed as mature, irrespective of details as regards age. From this we conclude that, in *Hæmenteria*, the somite has not yet reached the pentannulate condition, and further that this state would be reached by a division, evidently simultaneous, of each of the terminal or non-sensory annuli of the triannulate somite. The order of development of the annuli would then be :—

1	2	3	4	5
d	c	a	b	d

This order shows then again a variation from that which obtains in such pentannulate forms as *Hirudo*, and is intermediate between that which obtains in the latter forms and such forms as *Ozobranchus*, *Pontobdella*, *Orobdella*, and *Philæmon*. A point of further interest in connection with this is that the triannulate adult somite is the prevalent condition among the *Rhynchobdellidæ*, and the pentannulate among the *Arhynchobdellidæ*.

Hæmenteria is the only member of the *Rhynchobellidæ* which shows any trace of the pentannulate somite, and occupying an equally unique position among the *Arhynchobdellidæ* we find *Mesobdella* which is the only member of the latter group in which the adult somite is triannulate. Both these genera then serve as intermediate forms between the *Rhynchobdellidæ* and *Arhynchobdellidæ* in connection with the nature of the somite.

Summary.—From facts and statements given above, it may be concluded in general that the posterior region of the sensory somite is first affected in connection with somite-extension. Further divisions may affect the posterior region exclusively as in *Semilageneta* and *Geobdella*, but in the majority of cases we find the anterior similarly affected. The fact that the division is proved to be restricted to the posterior region in some forms is not astounding, (and is very interesting in keeping with the fact that the posterior annulus of the biannulate somite is the first non-sensory annulus developed in that it shows a distinct stimulus behind this region) in regard to division, and inasmuch as considerable variation takes place in the evolution of the multianulate condition of the somite is but to be expected. In the majority of forms, however, as stated above, the anterior portion of the somite is affected after the addition of the first posterior annulus. Later divisions typically affect both extremities, or in some cases may be restricted, at least for a time, to the anterior extremity. Examples of the latter are to be found in those leeches in which the adult somite is tetrannulate. After the formation of terminal non-sensory annuli the sensory annulus is, as a rule, not affected, but sometimes is as a result of the inability of the terminal annuli to undergo further division.

In discussing the question of metamerism I have attempted to explain the nature of annulation in all the forms as the result of an action of extension. There is no scientific support behind the flat denial that "abbreviation" or fusion takes place. However, if such a process does occur, it is quite secondary in importance and by no means frequent in occurrence.

EXPLANATION OF PLATE III.

Figs. 1A, 1B, 1C,—Diagrams showing the arrangement of the annuli in the genital somite of *Orobdella Whitmani*, *O. Ijimai* and *O. octonaria* respectively, according to the scheme laid down in the text.

Figs. 2A, 2B, 2C,—Diagrams of the same, showing the annuli of the genital segments arranged according to Whitman's scheme.

Figs. 3A, 3B, 3C,—Diagrams showing the arrangement of the annuli in *Geobdella*, *Philaemon*, and *Pontobdella macrothela* respectively.

CONTRIBUTION TO A KNOWLEDGE OF AUSTRALIAN *HIRUDINEA*. Part vi.

The Distribution of the *Hirudinea*, with Special Reference to Australian Forms, and Remarks on their Affinities, together with Reflections on Zoogeography.

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Of the Australian forms enumerated in a list of species which I have made, at least five genera are characteristic of Australasia (in its ordinary geographical sense). Of these, three are aquatic genera—*Semilageneta*, *Dineta*, and *Hirudobdella*; the remaining two genera, *Geobdella* and *Philæmon*, are land-forms. From this it will be seen that we have characteristic generic representatives of the *Ichthyobdellidæ* (if *Semilageneta* must be allotted a position under the present classification), *Herpobdellidæ* and *Gnathobdellidæ*. Some little interest attaches to *Ozobranchus branchiatus* from a distributional standpoint, in that the only other known species of the genus is that noted by Apathy in the Mediterranean Sea. In connection with this, I have previously stated that this genus is evidently always associated, under parasitical conditions, with members of the Chelonia, in contradistinction to the confinement of species of *Branchellion* to the Pisces. *Chelone mydas*, the host of *Ozobranchus branchiatus*, is distributed over the Pacific, Indian, and Atlantic Oceans, so that, in all possibility, this member of the Hirudinea has a very wide distribution. Oka, in 1895, described a species from Japan which he doubtfully referred to *O. Mendesi*, and this, no doubt, is meant for *O. branchiatus*. Unfortunately I have not had the opportunity of reading Oka's original paper, and have gleaned my information from a reference made by Moore.

Branchellion, which is represented by at least three definite species in Australian waters, is a universally distributed genus, being noted from the Atlantic, Pacific, and Indian Oceans. *Pontobdella* is likewise a cosmopolitan form, and is represented by at least one definite characteristic Australian species, *Pontobdella australiensis*. *P. macrothela* was originally found by Schmarda in Jamaica, and Blanchard has noted the same species from Sumatra; so that the presence of this species in Australian waters would seem to indicate that it is universally distributed. *Semilageneta*, represented, up to the present time, by a single species known from no other part of the world, is interesting in that it is apparently intermediate between the Ichthyobdellid and Glossiphonid forms, as noted previously. No characteristic representative genus of the *Glossiphoniidæ* is to be noted in Australasia. Three genera, *Glossiphonia*, *Placobdella*, and *Microbdella* have been found, the former in Australia and Tasmania, the latter two in New Zealand. The occurrence of *Microbdella* in the latter place is interesting, in that it was discovered almost exactly at the same time as Moore discovered and described the type-species, *M. biannulata*, from Carolina, U.S.A. As I have previously pointed out, no terrestrial member of the *Rhynchobdellidæ* has ever been noted in any part of the world, and, in view of this, the occurrence of these freshwater forms in Australasia, in contradistinction to the limited distribution of the terrestrial members of the Hirudinea, serves as excellent corroborative evidence of the cosmopolitan distribution of freshwater forms of life, which is due, no doubt, to a great extent to the means of transmigration offered by birds, etc.

Among the *Herpobdellidæ*, we find in Australia the cosmopolitan genus *Herpobdella*, and a genus, *Dineta*, confined, so far as is known, to Australia. The latter form, however, as has been noted previously, is very closely allied to the former, and, again, both these genera are freshwater forms.

The Gnathobdellid representatives fall into two groups, viz., aquatic and terrestrial. Among the former are comprised representatives of three genera—*Limnobdella*, *Hirudobdella*, and

Hirudo. *Limnobdella australis* of Australia and *L. mauiana* of New Zealand are exceedingly closely allied, and apparently they differ only in colour-pattern, and perhaps slightly in dimensions. Their anatomy agrees in the points of difference as cited for the differentiation of the genus from the common genus *Hirudo*. Whether we regard them as distinct species or not, their distribution is of some interest. In support of this, we find in New South Wales a new genus, *Hirudobdella*, which was originally discovered by Prof. Benham in New Zealand, in the form *Hirudo antipodum*, which Prof. Benham himself thought must fall into a new genus. *Limnobdella* is known from other parts of the world, and so, like other freshwater forms, has a cosmopolitan distribution. *Hirudobdella*, represented up to the present by one New Zealand species and one Australian species, is also a freshwater form; and, probably, when viewed critically from the standpoint of distribution, is to be regarded as a highly modified subgeneric offshoot from the Hirudo-stock.

In considering the question of distribution, perhaps the most important members of the Australasian Hirudinea are the terrestrial genera, *Philæmon* and *Geobdella*. Before entering into a discussion of the affinity and distribution of these forms, it will perhaps not be out of place to point out the distribution of the terrestrial *Arhynchobdellidæ* throughout the world, with a view to pointing out the significance of their distribution in bearing on zoogeographical questions.

The number of terrestrial species is very small: so far only eight genera are known, five of which belong to the *Gnathobdellidæ* and three to the *Herpobdellidæ*. The former include:—

Hæmadipsa Tennent, 1861; Ceylon, India, Burmah, and Japan.

Xerobdella von Frauenfeld, 1868; mountains of Europe.

Mesobdella Blanchard, 1893; Chili.

Geobdella Whitman, 1886; Australia and New Guinea.

Philæmon Blanchard; Australia and Tasmania.

The *Herpobdellidæ* include:—

Cylicobdella Grube, 1871; South America and West Indies.

Lumbricobdella Kennel, 1886; South America and West Indies.

Orobdella Oka, 1895; mountains of Japan.

Forbes, in 1890, also recorded the occurrence of a terrestrial species, in North America, of the genus *Semiscolex*, whose members are generally aquatic.

In comparing now the distribution of these forms with that of aquatic forms, it will be seen that the former are much more limited and do not enjoy a cosmopolitan distribution.

The *Hirudinea* in general were probably derived from an aquatic ancestor; and, in view of the fact that the great majority of species are still aquatic in habit, we must regard the terrestrial forms as being specially modified for a terrestrial existence, or as having specially adapted themselves to an environment quite different from that under which the majority of the forms have maintained their existence.

It might be merely suggested that the adaptation of some forms to a terrestrial existence might be due to the adaptation of an aquatic host by evolution to terrestrial conditions. This suggestion would receive some weight from the argument, which is well supported, that the *Hirudinea* represent an archaic group. At the same time it is to be borne in mind that several of the terrestrial *Gnathobdellidæ* differ in only a small degree from certain allied aquatic forms of the same group.

In New Zealand, no land-leeches have yet been noted. Mr. Moore, of the United States National Museum, and Prof. Benham have shown definitely that the specimens of *Geobdella limbata* ascribed to New Zealand are identical with *H.* (*Chthonobdella*) *limbata* described by Grube from Sydney, and no doubt this represents the locality whence they were obtained. Further, land-leeches would certainly have been discovered long ago if they existed in the New Zealand bush. Two terrestrial genera have been noted in Australia, viz., *Philæmon* and *Geobdella.* Both these forms are very characteristic, and exhibit points of special interest. *Philæmon pungens* is the sole species known of that genus, and is to be found in Victoria and Tasmania, and in New South Wales. *Geobdella* is represented by three species—*G. australiensis*, *G. Whitmani*, and *G. tristriata*—the former two being present in New South Wales and Queensland, and the latter in New Guinea. This latter distribution is of interest from a zoogeographical standpoint. The fact that they are so confined in their distribution would seem to indicate with some certainty that the problem of migration of the species of these terrestrial forms is much more difficult than in the case of the aquatic forms, and that we may consider them, in their distribution, seriously in connection with zoogeographical schemes. Again, these forms are in all probability limited to the eastern side of the continent, the conditions of moisture, and the subtropical nature of a good part of this area being much more suitable for such forms of life. We may probably conclude from this that the genus *Geobdella* had a range extending from Australia through at least part of the once existing Austro-Malayan Peninsula, and that in all possibility sufficient time has elapsed since the separation of this land-mass from Australia to allow of the evolution of the New Guinea species, *G. tristriata*, which is quite distinct from the Australian forms, and like them is terrestrial. Further, we are also to regard *Philæmon* as being characteristic of the southern half of the old Australasian continent, including Tasmania, and *Geobdella* of the northern and more tropical half.

Perhaps I may be excused, preliminarily, before entering on a discussion of the affinities of these two genera, if I attempt to review in consideration the distribution of these forms with a view to demonstrating their antiquity. If we assume that the occurrence of one and the same species of *Philæmon* in Tasmania, Victoria, and New South Wales, is not due to the interference of mankind (and this assumption I strongly support later), then we must conclude that this genus once spread over the whole of these combined areas when a land-connection existed between Victoria and Tasmania, and further that inasmuch as only one species is known, the genus must be a distinctly archaic one. In support of this, we have the interesting fact that *Geobdella*, which, as will be pointed out later, is very closely allied to *Philæmon* and might very well, on many scores, be regarded as a subgenus, is confined to the northern half of New South Wales, Queensland and New Guinea. In considering, then, the distribution of these two genera, we are forced to conclude that both have been evolved from a common stock, and that *Geobdella* has adapted itself to tropical and subtropical conditions, and *Philæmon* to more temperate conditions.

I think that I may now reasonably suggest, if not conclude, that both forms are distinctly archaic. In concluding these remarks in their special reference to the question of distribution, it may be stated that one might reasonably have expected to meet with representative species of one of our Australian terrestrial genera in some of the Island groups to the east of Northern Australia which, many men of science, in consideration of the continental nature of the group, have suggested were connected as an extension in an easterly or south-easterly direction with the Austro-Malaysian Peninsula. When engaged in a collecting tour in Fiji some years ago, although I spent some months in active collecting in the thick bush of that region, I met with no member of the group, nor did I ever hear any reference made by natives, a vast number of whom rendered me every assistance possible in my work, and most enthusiastically proferred any information they had. Further, I know of no records from the New Hebrides. This leads one, at the least, to suggest that neither of the Australian forms found its way beyond New Guinea, either in an easterly direction or in a westerly direction. I have mentioned these details with a view to suggesting that our two Australian genera have arisen from a common Australian ancestor which was evidently not far removed from either of them in nature; and further, that this evolution has taken place since the splitting up and separation of the outer portion of the supposed peninsular continental mass but prior to the separation of New Guinea from Australia. Again, if New Zealand were ever connected in a northerly or north-easterly direction with any of the continental masses above mentioned, the absence of these forms in New Zealand is explained either by the fact that they never did spread to any distance in an easterly direction, or that this hypothetical connection with New Zealand is of enormous antiquity.

In discussing the relationship of the two genera, *Philæmon* and *Geobdella*, it is interesting to see that they show marked affinities, which in themselves are unique characteristics of the two genera, viz., the presence of only two jaws, and the same position of the eyes. These affinities must be seriously considered as representing certain fundamental characters common to both, and probably to be found in an ancestor common to both, inasmuch as one of these points, viz., that of the jaws, is a most important factor to be considered in connection with classification. At the same time there are wide differences between them which would seem to indicate that both forms have long been differentiated sufficiently for the generation of separate genera. I have pointed out, in connection with the subject of metamerism, in another chapter that in *Geobdella* the pentannulate somite has been derived from the uniannulate segment by the addition of four annuli posterior to the primitive ring, whereas in *Philæmon* the sensory ring is denoted by the third annulus of the tetrannulate somite, indicating that the order of origin of the annuli is quite different. The question is now to be considered whether this tetrannulate condition has been arrived at by the absorption of the last annulus of the pentannulate somite, as seen in *Geobdella* (or the pentannulate somite by the addition of another annulus to the tetrannulate somite of *Philæmon*); or whether these two forms were differentiated after the common ancestor had developed the biannulate somite. One finds that, in connection with somite-constitution, the chief change is that of extension, or in other words, the generation of the multiannulate condition. This we know definitely has taken place extensively in all members of the *Hirudinea* to a greater or less extent, but, at the same time, there is no substantial scientific support behind the denial that retrogressive changes ever take place, that is, that an abbreviation may take place secondarily. If one removes the last annulus of the pentannulate somite of *Geobdella*, it will be seen that the sensory annulus would not occupy the same position as that seen in *Philæmon*, with its tetrannulate somite; or again, by adding another annulus to the somite of *Philæmon* the pentannulate somite of *Geobdella* would be obtained; but the position of the sensory annulus would not correspond in both.

It must, of course, be borne in mind that although the number of annuli in the whole body is different in the two genera—79 in *Philæmon*, 95 in *Geobdella*—and the peculiar positions of the genital apertures in *Geobdella* are of great importance, their anatomy agrees very closely.

The total number of annuli in the body is dependent on the fact that one is pentannulate, and the other tetrannulate, and this may explain to some extent also the peculiar relative positions of the genital apertures in *Geobdella*, which at first would seem to be of such great importance.

In view of what I have stated in connection with metamerism and the importance of the order of origin of the annuli in discussing genetic relationships of leech-forms; and taking into consideration what I have stated as conclusions to be drawn from a study of the distribution of these two forms as a reflection of their archaic nature; seeing that the order of origin of the annuli is so different in these two forms; I conclude that they have been derived from a common ancestor which agreed very closely with them in regard to the jaws, position of the eyes, and general anatomy, but which, at the time these two genera were differentiated, had not developed a somite of more than two annuli.

In conclusion, I may state that the remarks which have been made in this paper in regard to the conclusions to be drawn from the distribution of our terrestrial *Hirudinea* in regard to zoogeographical schemes, are in keeping with those which the distribution of Monotremes, Marsupials, and Peripatus, etc., has long since justified. In this direction I have, then, merely added corroborative evidence from a study of the *Hirudinea* themselves, and have hopes that I have conclusively pointed out that the terrestrial members in general of the *Hirudinea* serve as good types to be considered in connection with a study in zoogeography.